On the relation between niche overlap and competition: the effect of incommensurable niche dimensions

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Summary. Questions about the relation between niche overlap measured along single niche dimensions and total niche overlap, and about the relation between overlap and competition, have long troubled ecologists. In this note it is shown that competition may exist even though overall niche overlap in a multidimensional niche space is zero. A distinction is drawn between niche dimensions which describe the various attributes of a single basic resource category, such as food, and niche dimensions which describe functionally distinct ways in which the environment influences the fitness of an organism. Examples of the latter kind of niche dimension include potential limitation by two or more qualitatively distinct resources, and axes describing resource use and escape from predators. The relation between overlap and competition may be complex if niche dimensions reflect qualitatively distinct ways that the environment affects fitness, and, in particular, competition may exist despite zero total overlap in a multidimensional niche space.

Introduction

Hutchinson's (1957, 1978) geometric characterization of the ecological niche is one of the most familiar conceptual constructs in ecology. Despite shifts in the meaning of the word "niche" (Hurlbert 1981), and occasional suggestions that the term be dropped altogether from the ecological lexicon (Williamson 1972: 111), discussions of the multidimensional niche concept still permeate both textbooks of ecology (e.g., Ricklefs 1979, Begon and Mortimer 1981, Pianka 1983) and the primary research literature (e.g., Pianka 1973, 1975, 1981, Pianka et al. 1979, Pacala and Roughgarden 1982). The niche of a species may be defined abstractly as a fitness measure in a multidimensional environmental space (Levins 1968). More concretely, niches may be characterized as measures of resource utilization (Pianka 1983, Giller 1984). The niche concept has been used both as a tool for systematically describing the major environmental variables influencing the distribution and abundance of single species (Maguire 1973, James et al. 1984), and as a device for understanding interspecific interactions and community structure (Pianka 1981), particularly in the theory of limiting similarity (Abrams 1983).

One problem that has troubled both theoreticians and empiricists is how to relate the overlap of Hutchinsonian niches to interspecific competition. Schoener (1983) has observed that in experimental studies of competition, overlap in microhabitat or food tends to be positively associated with competition, whereas macrohabitat overlap often is not. Rosenzweig (1981) has demonstrated theoretically that habitat selection may lead to habitat partitioning (zero spatial overlap) between a pair of species such that, at equilibrium, competition cannot be detected by the usual sort of perturbation experiment – yet the partitioning exists only because natural selection favors individuals that escape interspecific competition.

A second vexatious issue has been the question of how to relate overlap along each of several niche dimensions to the true overall niche overlap, which is usually only seen (as though through a field glass darkly) by its projections onto various niche axes (Pianka 1973, 1975, 1981, Cody 1974, May 1975, Harner and Whitmore 1977, Slobodchikoff and Smith 1980). Several recipes for combining unidimensional overlap measures into estimates of multidimensional overlap have been proposed. For example, May (1975) suggests that if the utilization of resources along each niche dimension is independent of utilization along the other dimensions, multidimensional overlap can be estimated as a product of unidimensional overlaps.

"Niche overlap refers to the utilization of some of the same resource type by two or more species of resource consumers". (Abrams 1980). Fig. 1 shows a version of the usual textbook representation of overlap between a pair of species in a two-dimensional niche space, (see, e.g., Pianka 1983: 264–265) where for simplicity each species is assumed to have a uniform distribution of utilization within its rectangular fundamental niche. In Fig. 1 (left), the overlap seen on the projections along *each* axis reflects the true overlap in the multidimensional niche space; in Fig. 1 (middle) the projected niches overlap without there being any overall overlap; in Fig. 1 (right), the two niches are so dissimilar that there is overlap neither for the projections along any single niche dimension nor in the total niche space. The point of the figure is that if there is overlap in the full, multidimensional space, then there is necessarily pro-
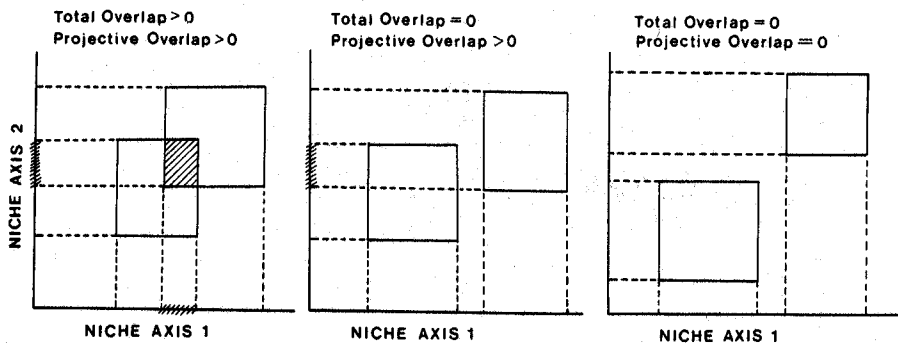
Fig. 1. Relationships between total niche overlap and projective overlap. The fundamental niches are drawn for two species in a two-dimensional niche space. (left) Overlap in the multidimensional niche space necessarily implies overlap between the niche projections of the two species along each axis. (middle) Conversely, niche projections may overlap with zero total overlap. (right) Species may be so dissimilar that there is neither total overlap nor projective overlap.

jective overlap along each axis; zero overlap along *any* axis thus implies zero total overlap.

A common protocol in observational studies of communities is to carry out natural history studies of sympatric species (typically a phylogenetically defined taxon: genus, family, etc.), recording habitat use, food type utilization, and temporal activity patterns. Habitat, food type, and time (in that order of importance) are the three principal kinds of resource-partitioning differences usually observed (Schoener 1974a, 1986). The problem I address here may arise whenever one combines habitat data and food utilization data into a compound measure of overall niche overlap between species, and then attempts to draw inferences about competition from these overlap measures. I will argue that this procedure assumes that habitats are important principally as functionally de-coupled arenas for competition, and that food is the only resource over which competition is occurring. Whenever competition is potentially occurring for both food and a qualitatively different resource (e.g., nest sites), interspecific competition may exist even though overall overlap in a multidimensional niche space is zero. The basic points I wish to make are quite simple, and I suspect widely known among practicing community ecologists, but I have not found them clearly articulated in the vast literature on niche overlap indices.

Competition with zero multidimensional niche overlap

Is multidimensional niche overlap necessary for the existence of interspecific competition? No. Let us assume the contrary, so that if two species are competing, then their fundamental niches (or bivariate utilization functions) must show geometrical overlap as in Fig. 1 (left). As stated above, it follows that the projections of the niches onto *each* niche dimension must also overlap (see Fig. 1 (left)). In turn, if the niche projections do not overlap along even a single axis, overall overlap must necessarily be zero, too, and, by assumption, the

two species cannot be competing. But there are many biologically plausible situations in which multidimensional overlap is zero, for instance because of complete niche separation along one niche dimension, and competition nonetheless occurs. Here I briefly outline two. One was identified by MacArthur (1968: 160), who stated that "The statement 'two species coexist if their niches do not overlap' [is] plausibly false, since by feeding in different places, two species would occupy nonintersecting niches even if they both depended on and competed for the same highly mobile food supply". Thus, habitat partitioning may not, in fact, separate distinct arenas of competition.

For instance, Huey and Pianka (1981) note that sit-and-wait lizards principally encounter and eat active, mobile prey. A lizard that is specialized to one habitat may reduce the flux of mobile prey into other habitats, inhabited by another species of lizard, and hence exert a competitive influence at a distance. Similarly, hermit crabs are often habitat specialists, and their populations may be limited by the availability of empty snail shells (Vance 1972). Because abiotic forces and crab mobility move shells among physically distinct habitats, habitat segregation does not preclude competition. Hazlett (1981: 16) notes that because of this resource motility, "hermit crabs living in the marine and terrestrial environment may exploitatively compete with each other, perhaps more than species within one environment".

This kind of problem arises because one has an inadequate understanding of the natural history of the resource base over which competition is occurring. After all, given that one believes resource competition to be the dominant force structuring a community, the fundamental purpose of identifying niche dimensions is to discriminate independently renewing resource populations (Schoener 1974a, 1986), the differential use of which may promote species coexistence. In the above examples, the habitat dimension does not adequately separate independent resource populations.

A quite different and potentially more serious prob-

lem may arise whenever different niche axes describe the utilization of qualitatively different resources. Consider the potential modes of interactions between a pair of Central American *Myiarchus* flycatchers. These birds commonly nest in cavities or excavations made by other birds and feed on aerial prey. In Fig. 1, the x-axis could describe some aspect of nest quality (e.g., hole size), and the y-axis a linearly orderable property of prey. Resource use along the two axes could be statistically independent, so that if $f_i(x)$ describes the utilization of nest sites by species i, and $g_i(y)$ its utilization of prey, the bivariate function $u_i(x,y) = f_i(x)g_i(y)$ formally describes the joint utilization function of both prey and nests. Two co-occurring species of *Myiarchus* could use completely different nest sites and perforce have zero multidimensional overlap, yet obviously still compete fiercely for prey.

The central feature of this hypothetical example is that one has conflated qualitatively distinct resource categories, both required for fitness, into a single utilization measure. The practical problem is that when one combines habitat use information with dietary information into a single index of niche overlap, one implicitly assumes that habitats are principally important as places to acquire food. In many environments, however, habitat axes may describe resources other than food or reflect the influence of natural enemies.

For example, Culver (1973, 1982) has extensively explored interspecific interactions in aquatic cave communities. He reports that both amphipods and isopods are found in riffles under rocks and pebbles, sites which simultaneously provide refuge from mortality factors (both washout in the current, and salamander predation) and places to feed. The food supply in cave streams is typically quite low, so an amphipod and isopod could compete exploitatively for limited food resources. Culver performed experiments and showed that there is also direct competition for access to refuges. To understand niche separation in these communities, we must examine overlap along both refuge and prey size axes. But the overall, bivariate niche overlap between an isopod and amphipod could well be zero, in an abstract niche space with axes characterizing prey and refuges, because of (say) zero overlap in prey sizes used, even though competition is quite intense due to overlap in refuge use.

This same point may apply quite generally to any system in which species simultaneously depend upon a shared resource base and share mortality agents such as predators, parasites, or pathogens. For instance, Lawton (1978) remarks that the architecture of a terrestrial plant may influence the diversity of co-occurring phytophagous insects in two distinct ways. First, the various parts of the plant may provide niche axes along which species may segregate in the classical way to avoid competition for resources. Secondly, the avoidance of predation or parasitism may result in what amounts to competition for refuges ("enemy-free space", Jeffries and

Lawton 1984). A strong numerical or aggregative response by predators is expected to produce (–,–) interactions among alternative prey species (Holt 1977, 1984), even if prey subsist on nonoverlapping food resources. A full understanding of any community influenced by both predation and resource competition requires analyses of niche relations along axes that order predator avoidance strategies, as well as along axes that describe resource utilization, and an understanding of how these axes interact to determine species coexistence. In like manner, recruitment in a plant community may depend upon light, inorganic nutrients and other factors determining productivity, and pollination. Competition for pollinators may occur in the absence of, or alongside, more traditional kinds of competition for resources (Rathcke 1983). Without a detailed understanding of the natural history of the community, it may be difficult to exclude the possibility that a resource other than food is important in determining patterns of habitat utilization. This suggests that one should be cautious about interpreting overlap measures which combine habitat and dietary information into a single number.

Discussion

A single measure of overall niche overlap clearly cannot encapsulate the diverse modes of interspecific interactions simultaneously operating in the systems described above. These observations do not imply that overall overlap measures are valueless. At the very least, such measures provide compact descriptions of community patterns, even if the measures cannot be related in any simple fashion to particular mechanistic models. Moreover, zero total overlap may at times actually imply that there can be no competition. Much of the discussion in the ecological literature about multidimensional niches, and the need to infer total overlap from partial overlaps, implicitly or explicitly assumes that competition is occurring for one kind of resource – food – and that overlap measures the common utilization by a species pair of this basic resource category. For instance, Pianka et al. (1979) discuss the properties of a resource matrix "with each entry representing the probability of capture of a prey item of a given size at a particular height". Species may avoid competition for food by selecting prey of different sizes, or by feeding in different places, or possibly by foraging at different times (but see Schoener 1974b) (although one should be alert to the problem of non-independent resource populations noted by MacArthur (1968)). In this case, the niche dimensions are just different attributes of a single resource type, food, the acquisition of which is related to fitness. If the system under study is governed by competition for a single resource category, overall niche overlap may bear some simple relation to interspecific competition, because it summarizes concisely the cluster of dimensions required to adequately discriminate the resources used by coexisting consumer populations.

In the case of bird ecology, for instance, Lack (1954, 1966) forcefully argued that food availability played a dominant role in avian population dynamics. This position legitimized a generation of work on bird communities based upon the presupposition that competition for food underlies both patterns of habitat partitioning and segregation by prey type (but see Wiens 1983).

By contrast, if one niche axis actually ranks prey by size, another measures nest site quality, a third describes escape from predation (by means of activity time), and so forth, then even if the observed utilizations along each axis are statistically independent, the niche dimensions are in a sense *incommensurable* except in the ultimate currency of fitness, because they describe different components of fitness or qualitatively different resource categories. (This is not to say that incommensurable niche dimensions are non-interactive; for instance, the habitats in which an organism forages may determine the predators it is exposed to.) More generally, describing the utilization of each qualitatively distinct resource category may require a cluster of dimensions. The kind of dimensions used to describe the different clusters might even overlap. With certain sets of niche dimensions, however, it will usually be inappropriate to relate overall overlap measures in a full multidimensional niche space to interspecific competition, for the simple reason that competition may occur despite zero overall overlap. The theoretical, as opposed to the descriptive, utility of measures of overall niche overlap thus depends upon whether a single factor (e.g., food limitation) with multiple descriptive attributes is of overwhelming importance, or if instead multiple, qualitatively distinct factors might be operating. When all is said and done, there is unfortunately no substitute for attempting to grapple with the mechanistic basis of the resource-consumer interactions underlying interspecific competition (Tilman 1982, Abrams 1983).

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